A PHYLOGENETIC TEST OF ACCELERATED TURNOVER IN NEOGENE CARIBBEAN BRAIN CORALS (SCLERACTINIA: FAVIIDAE)

by KENNETH G. JOHNSON

ABSTRACT. Documenting patterns of long-term faunal change is an important application of palaeontological data, but questionable results may be obtained if the potential effects of sampling bias are not considered. Analysis of fossil Caribbean reef coral occurrences indicates significant species turnover during the late Neogene. The goal of this study is to test this pattern for a subset of the entire fauna by using phylogenetic information to identify problematical taxa and periods of poor sampling. A phylogeny for 40 species from the faviid genera *Caulastraea*, *Colpophyllia*, *Diploria*, *Favia*, *Hadrophyllia*, *Manicina* and *Thysanus* was inferred using 23 multistate characters. Although the relationships are homoplasious, some stable groups emerged. One group includes the *Colpophyllia* species, another includes *Manicina*, *Hadrophyllia* and *Thysanus* species. As currently defined, both *Favia* and *Diploria* are paraphyletic stem groups. The inferred evolutionary tree was used to estimate species richness and proportional origination and extinction rates. When ghost lineages are considered, the magnitude of species richness estimates increases resulting in lower estimates of proportional origination and extinction. However, the pattern of faunal change within the group remains largely unchanged, with increased origination during the Late Miocene followed by extinction during the Late Pliocene and early Pleistocene.

PALAEONTOLOGICAL data are used to document patterns of long-term faunal change. As such they provide the primary data to assess the rôle of potential causes and to develop predictions of the potential consequences of periods of rapid turnover in the history of life. However, bias in sampling can lead to inconclusive or misleading results. Two strategies have been applied to overcome artefacts due to incomplete or uneven sampling (Smith 1994). One approach is to compile occurrences of high level taxa such as genera or families, and use these data to estimate taxonomic ranges. The distribution of ranges through time can then be analysed using evolutionary metrics. By including large numbers of taxa in their analysis, proponents of this approach are able to detect large-scale patterns free of sample bias. Supraspecific level taxa are likely to be better sampled (Gilinsky 1991), but suffer from problems of definition and comparability (Eldredge and Cracraft 1980) because they usually are defined as arbitrary subdivisions of a particular lineage rather than as holophyletic groups.

An alternative approach is to compare stratigraphical occurrence patterns at low taxonomic levels with phylogenetic information (Novacek and Norell 1982). Stratigraphical evidence has been widely used to test hypotheses of phylogeny. For example, the stratocladistic method proposed by Fisher (1991) explicitly includes stratigraphical information into the procedure for comparing competing hypotheses of relationship. Conversely, phylogeny can be used to assess the rôle of biased sampling in generating apparent patterns of faunal change (Benton 1994). Combining stratigraphical and phylogenetic data in an evolutionary tree will usually require interpretations of 'ghost lineages' and hypothetical range extensions (Norell 1992). Therefore, the estimates of rates of taxonomic evolution can change when phylogenetic information is included in an analysis of diversity patterns.

Recent work has provided evidence for rapid change in the Caribbean reef coral fauna during the late Neogene (Budd *et al.* 1996). Accelerated species turnover has been documented using a

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comprehensive compilation of all known reef coral occurrences from over 70 Miocene to Recent localities (Budd *et al.* 1992). Study of the patterns of species first and last occurrence using this database indicates a significant turnover event in the Late Pliocene to Pleistocene, with extinction rates as high as 30 per cent. of the fauna per million years during the late Pliocene. Furthermore, study of extinction selectivity among ecological groups indicates that species with small, short-lived colonies which reproduce sexually have overall higher rates of origination and extinction throughout the Neogene (Johnson *et al.* 1995). The origination and extinction of these types of taxa is the main mode of faunal change in late Neogene Caribbean reef corals. The goal of this study is to test the hypothesis of accelerated Pilo-Pleistocene faunal change by including phylogenetic information in the analysis.

There are over 170 species in the complete database, so developing a baseline phylogeny of the entire fauna is a prohibitively large task. Instead, a phylogeny has been inferred for the subset of taxa which experience the highest turnover. Most of these taxa come from the Faviidae, and have been classified into seven genera in which colonies form through primarily intratentacular division (Vaughan and Wells 1943). Three of these genera are restricted to the Caribbean region (*Manicina*, *Hadrophyllia* and *Thysanus*) whilst the others (*Caulastraea*, *Colpophyllia*, *Diploria* and *Favia*) have a broad geographical distribution including Mediterranean and Pacific occurrences. Several of the genera (*Manicina*, *Hadrophyllia*, *Favia* and *Thysanus*) include species which tend to live as small, free-living colonies in off-reef and reef marginal environments.

Previous attempts to reconstruct coral phylogeny using explicit cladistic techniques and skeletal characteristics have been hampered by the presence of excessive homoplasy and therefore poor resolution of species relationships (e.g. Budd and Coates 1992). But even homoplasious characters can be used to define groups (Pandolfi 1989), and analysis of skeletal characteristics on living material has been shown to be substantially in agreement with analyses of molecular and soft tissue characteristics (Potts *et al.* 1993; Budd *et al.* 1994). Furthermore, some workers (Veron 1995) have suggested that hybridization among disparate coral taxa is possible and has occurred repeatedly in the evolution of the Pacific coral fauna. If this is the case, then inferring phylogeny using parsimony is clearly an inappropriate approach for this group. Regardless, the cladistic approach applied to corals in this work resulted in useful interpretable hypotheses of relationships among the study taxa.

A cladistic analysis is used to reconstruct the phylogeny of meandroid faviid corals. The inferred phylogeny includes a high degree of homoplasy but groups are relatively stable. By combining the inferred phylogeny with the stratigraphical distribution of the study taxa, an evolutionary tree is constructed for the group with implications for evolution and biogeography. The tree suggests that the Caribbean fauna was largely isolated from the Mediterranean by the Miocene, and subsequent evolution was primarily moulded by extinction of Mediterranean lineages and radiation of Caribbean lineages.

Adding ghost lineages and extinctions resulting from cladistic branching events to analysis of faunal turnover does not alter the general pattern of increased richness and turnover in the late Neogene. Obviously, including ghost lineages will increase richness estimates, and, in general, decrease estimates of per taxon rates of origination and extinction. Proportional rates of species origination remain constant throughout much of the late Paleogene and Neogene, but decrease during the Pilo-Pleistocene. This pattern is similar whether or not ghost lineages and range extensions are included. Similarly, the pattern of variation in species extinction is not changed by considering phylogenetic information. Although estimates of the rate of both background origination and extinction are lower when range extensions and ghost lineages are included, estimates of the magnitude of the late Neogene period of accelerated extinction are comparable.

PHYLOGENY

Taxa

A total of 40 species from the Faviidae has been included in the present analysis (Appendix). Taxa with Neogene and Recent distributions were taken from a comprehensive compilation of Caribbean

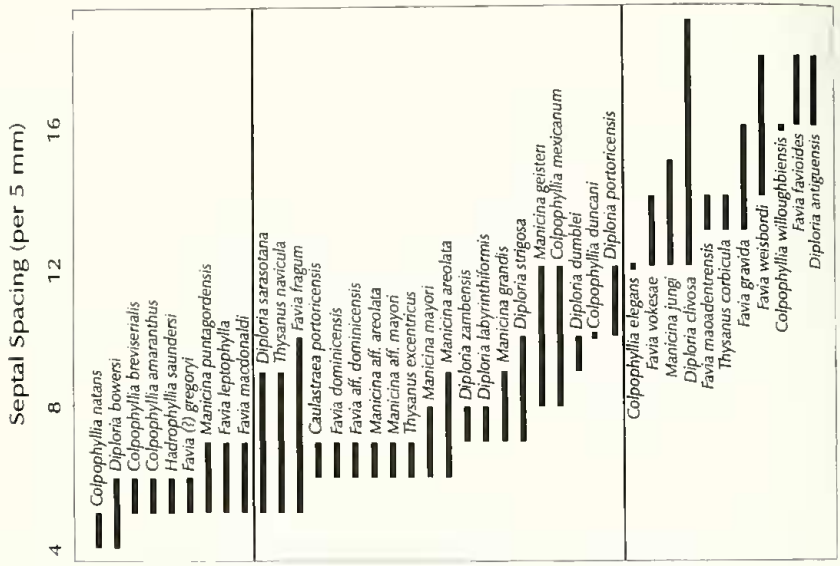
TABLE 1. List of characters included in the analysis including the type of character (discrete or continuous), *a priori* ordering of character states (ordered or unordered), and the number of character states. Measures of character fit (consistency index (CI) retention index (RI) and rescaled consistency index (RC) on the consensus cladogram are also listed. These are in general minimum estimates across the range of all 72 equally parsimonious trees. Amb. = ambiguous.

Character	Type	Order	States	Amb.	CI	RI	RC
1. Attachment of skeleton	D	U	2	Y	0·25	0·70	0·17
2. Meandroid series sinuosity	D	U	3	Y	0·40	0·77	0·31
3. Frequency of wall development	C	O	4	N	0·50	0·92	0·46
4. Symmetry of bud geometry	D	U	3	Y	0·40	0·50	0·20
5. Calicular platform shape	D	U	2	Y	0·13	0·50	0·06
6. Calice relief	C	O	4	N	0·21	0·54	0·12
7. Calice or valley width	C	O	4	N	0·25	0·74	0·19
8. Epitheca	D	O	3	N	0·20	0·67	0·13
9. Relative costa thickness	D	U	2	Y	0·20	0·43	0·09
10. Coenosteum	C	U	5	Y	0·31	0·59	0·18
11. Exothecal dissepiments	D	O	2	N	0·33	0·60	0·20
12. Costa continuity	D	U	2	N	0·13	0·50	0·06
13. Complete septal cycles	C	O	4	N	0·17	0·35	0·06
14. Septal spacing	C	O	3	N	0·13	0·28	0·04
15. Septal thickness	D	U	2	Y	0·10	0·40	0·04
16. Columella width	C	O	3	Y	0·20	0·69	0·14
17. Columella continuity	D	U	2	N	1·00	1·00	1·00
18. Septal lobes	D	U	2	N	0·50	0·83	0·42
19. Paliform lobes	D	U	2	N	0·11	0·56	0·06
20. Endothecal dissepiments	C	O	3	Y	0·15	0·58	0·09
21. Wall structure	D	U	2	N	0·50	0·94	0·47
22. Double or single paratheca	D	U	2	N	0·33	0·75	0·25
23. Maximum colony size	C	U	3	N	0·25	0·70	0·18

Neogene coral occurrences (Budd *et al.* 1994). Several new taxa from the upper Neogene of the Dominican Republic (Budd and Johnson 1998) have also been included. Paleogene taxa were obtained from lists included in a review of the Eocene Caribbean faunas (Budd *et al.* 1992). Eocene species from Jamaica (Wells 1935; Zans *et al.* 1962), and Oligocene material from Antigua and Puerto Rico (Vaughan 1919; Frost and Weiss 1979; Frost *et al.* 1983) have been taken from published lists and new collections. The Paleogene and early Miocene fauna from Chiapas, Mexico (Frost and Langenheim 1974) was also considered. All extant Caribbean species from the seven genera as well as endemic species from the distinctive Brazilian fauna (Verrill 1901) were included. However, congeners from the Pacific and Mediterranean faunas have not been included. Although the exact biogeographical relations between the Mediterranean, Caribbean and Pacific biotas are not well understood, none of the included taxa has been described from outside the Caribbean Basin. However, Frost (1977) briefly compared the Mediterranean and Caribbean Oligocene faunas and suggested that some taxa might be synonymous, but he did not complete a full revision of the faunas. Species classified into *Favia*, *Diploria*, and possibly *Colpophyllia*, have been described from the Mediterranean.

Characters

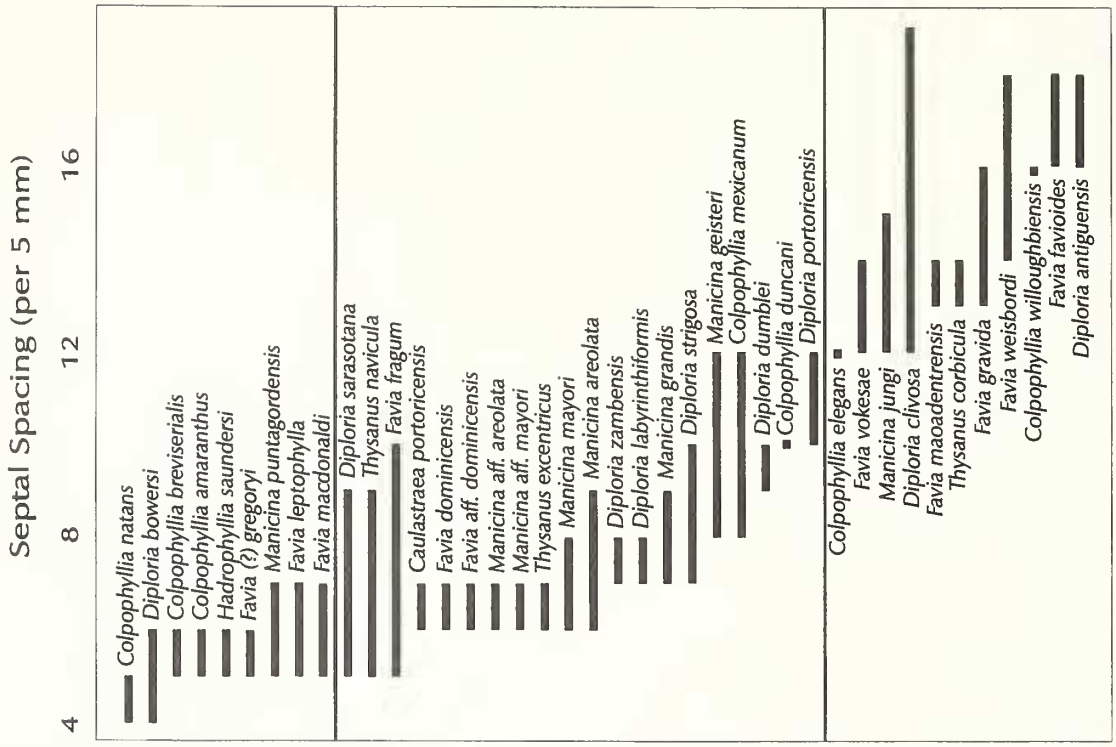
Skeletal morphology was characterized using 23 characters with a total of 64 discrete character states (Table 1) scored from type material when possible. When type material was not available, characters were scored from published descriptions and examination of material in museum



TEXT-FIG. 1. Distribution of septal spacing among the study taxa. Cut-offs to create discrete character states from this semi-quantitative measure were selected by visual examination of the distribution. Gaps are suggested at six and 12 septa per 5 mm resulting in three groups of species.

collections. Many of the characters are summaries of continuous variation in colony or corallite form which may not fall into non-overlapping (discrete) character states. Although some workers have criticized the use of characters with overlapping variation in phylogeny reconstruction (Chappill 1989), coral morphology is notoriously poor in features which are expressed as a few clearly non-overlapping states, so relationships among the study taxa are unlikely to be resolved if these attributes are not included. However, previous studies which used both overlapping and non-overlapping characters suggest that overlapping characters are more likely to be homoplasious (Stevens 1991).

A modified version of simple gap coding (Archie 1985) was used to subdivide continuous character distributions into discrete character states. The data for character coding are derived from a combination of measurement of type and accessory material and published species descriptions. Approximate ranges for each measured character were ranked by their midpoints, and plots examined for gaps in the character frequency distribution (Text-fig. 1). Where gaps were not evident, character state boundaries were defined at all levels where few taxa possessed ranges of variation which crossed the boundary between character states. Choosing the number of character states is a compromise between maximizing information content and maintaining consistency between characters (Archie 1985). Increasing the number of character states in a particular character increases that character's potential to resolve more groups but simultaneously increases the likelihood of homoplasy as random error in character scoring may obscure any phylogenetic signal. The division of a continuous character into discrete states remains an arbitrary act, but greater division of a character will not result in conflicting hypotheses of relationships (Thiele 1993).



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Coding a larger range of character states will increase tree resolution, but this resolution is likely to be unstable.

Each character was assigned equal weight in the analysis regardless of its range. Determining the range of a character was an important aspect of character selection and scoring, and therefore already involved many *a priori* assumptions regarding character weighting. Adding additional assumptions to the analysis will only decrease the parsimony of the resulting hypothesis, and cannot add any additional information into the analysis (Farris 1990). Characters have been ordered where there is a clear set of steps between the states, but other characters were left unordered. Characters were not explicitly polarized prior to the selection of the most parsimonious tree. Instead, an outgroup was included in the analysis and the shortest unrooted trees including both an ingroup and an outgroup were subsequently rooted at an internal node with a basal polytomy (Maddison *et al.* 1984).

Character states

Analysis of character states is arguably the most important component of any phylogenetic analysis, so considerable space is devoted here to discussion of how coral morphology was reduced to a set of characters with discrete character states. A complete list of character states scored for each taxon is included in the Appendix.

1. *Attachment of skeleton.* Almost all reef-corals live permanently attached to a hard substrate, a few taxa are free-living during most of their lives. As in all scleractinian corals, a pelagic (or motile benthic) larval stage settles on a hard substrate prior to skeleton development. However, two strategies exist which allow free-living species to avoid permanent attachment. In some taxa, the original attachment points are small pieces of rubble (especially skeletal plates from the calcareous green algae *Halimeda* sp.), and as the coral grows, the lower surface becomes larger than its attachment substrate and so becomes effectively free on the sea floor. In other cases, colony attachment points are not well developed, and the colony is broken loose either by physical or biological agents. In either case, the strategy allows populations to live in habitats with high sedimentation (Gill and Coates 1977). *States*: 0 = free-living; 1 = attached.

2. *Meandroid series sinuosity.* Meandroid series result from intramural budding which is not followed by the construction of walls between daughter polyps. In meandroid colonies, the orientation of budding and subsequent extension of polyps is expressed in the meander form of the colony. Sinuosity of the meander valley ranges from straight to sinuous, but no intrinsic order is obvious from the geometry of colony formation. Therefore, this character has been left unordered in the analysis. If the meandroid series is branching, this character refers to the nature of the valley between branching points. This character has not been scored for phaceloid, plocoid, or cerioid taxa because the budding history cannot be clearly assessed from the arrangement of corallites on the surface of a colony. For these taxa, this character has been scored as missing. *States*: 0 = mostly straight; 1 = greatly curved; 2 = sometimes sinuous.

3. *Frequency of wall development.* All taxa considered in this analysis utilize intramural fission to some degree during colony development. However, various colony forms may be constructed depending on whether walls are erected between sister polyps. Phaceloid, plocoid and cerioid forms result when walls are constructed after the formation of a new bud, whilst flabellate and meandroid colonies result when walls develop only occasionally. However, strictly meandroid or cerioid/plocoid forms occupy the ends of a continuum of colony forms. The character is best coded by counting the number of continuous valley sections in a colony relative to the number of growth centres (stomodaea). Because soft tissue is not preserved in extinct taxa, this character was scored

by estimating the relative lengths of continuous sections of meander valley. This is a more-or-less continuous character, so there is some scope for variability with taxa, especially considering that mechanical damage to colonies during life can divide continuous series and trigger the formation of new calical walls during recovery and overgrowth of the damaged region. However, the terminal states (no new walls compared with inevitable wall development) is generally invariable within species. *States*: 0 = walls always develop; 1 = walls develop in most (approximately two-thirds) new buds; 2 = walls develop in few (approximately one-third) new buds; 3 = walls never develop between new buds.

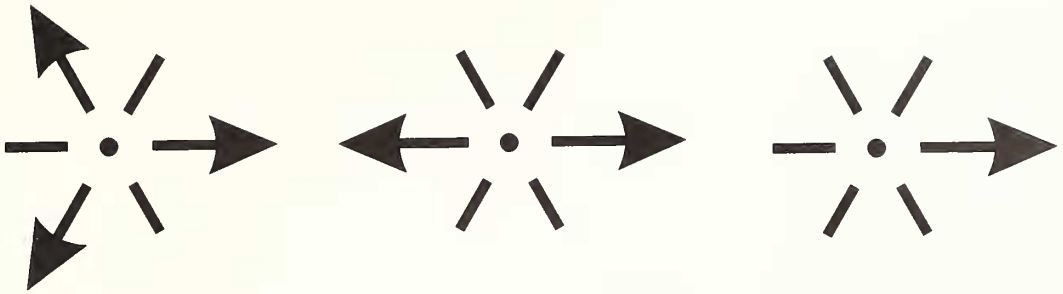
4. *Symmetry of bud geometry*. Scleractinian polyps are characterized by hexagonal symmetry, so new centres may develop in any one of six directions. However, in many meandroid forms, the direction of budding is geometrically constrained to one, two or three directions (Text-fig. 2). Meander valleys in taxa that are constrained to uni- or bi-directional growth are straight or sinuous single series resulting in a flabellate colony form. If tri-directional growth is possible, branching meander series can develop. Morphometric analysis of colonies of *Manicina areolata* suggests that polyps may be polymorphic with respect to budding direction. In *M. areolata*, stomodaea are invariably located over branching points in the meander series, but can also be positioned between branching points, and new centres may originate on the margins or interior to meandroid series. However, as new centres which develop internally are limited to bi-directional grow, new branch points are invariably added to at the ends of the meander series. This character was illustrated by Matthai (1926) who distinguished between stomodaea which form in linear series by repeated intra-tentacular budding on the distomodaeal mode and stomodaea formed by dichotomous branching or terminal forking. *States*: 0 = only uni-directional; 1 = only bi-directional; 2 = sometimes multi-directional.

5. *Calicular platform shape*. In the taxa considered here, septa are elevated above the columella and provide support for tentacle attachment. When the polyp is completely retracted into the 'valley', the soft tissue is protected by the septal plates. The margins of the septal may be gently inclined to nearly vertical. Variable preservation of the study material results in uncertainty regarding this character in some of the less abundant species. *States*: 0 = sloping or V-shaped; 1 = steep-sided or U-shaped.

6. *Calice relief*. This character describes the difference in elevation (relative to the upward growth direction) of the columella and the upper surface of the septa. It is a semi-quantitative character with numerical ranges defined by dividing the range along approximate discontinuities in the distributions measure material. However, in some cases, material was excessively worn or damaged, so measurements might be considered as minima, and the character state assignment might be questionable. Because of its inherent order, this character has been left ordered in the analysis. *States*: 0 = low (< 2 mm); 1 = medium (2–4 mm); 2 = high (4–10 mm); 3 = very high (> 10 mm).

7. *Calice or valley width*. This semi-quantitative character describes the wall-to-wall distance across a meandroid valley or corallite diameter in non-meandroid colonies. It is roughly equivalent to two times the major septal length plus the width of the columella, and is closely conserved within the meandroid species. Previous work on cerioid faviids (*Montastraea*) suggests that this character is perhaps the most useful diagnostic for recognizing reef-coral morphospecies within generic groups (Budd 1993). Assuming that the character states really fall along a continuum, this is included as an ordered character. *States*: 0 = small (< 5 mm); 1 = medium (5–10 mm); 2 = large (10–15 mm); 3 = very large (> 15 mm).

8. *Epitheca*. In the meandroid faviids, the epitheca is a distinctive non-trabecular thecal tissue deposited in a modified cavity on the perimeter of the skeletal secreting layer (Sorauf 1972; Stolarski



TEXT-FIG. 2. Illustration of three modes of bud geometry in meandroid faviid corals.

1995) which is thought to provide a protective cover for exposed skeleton. Such a function would be crucial for free-living corals in reef-marginal environments to deter infestation of boring organisms. Environmental variation may be significant in this character, but the states are general enough to include intraspecific variation. In several cases, outer surfaces of a colony were not preserved, so this character is coded as missing. *States*: 0 = absent or very reduced; 1 = reduced; 2 = well-developed.

9. *Relative costae thickness.* The relative thickness of major and minor costae may be equal, but in some forms, minor (third and fourth order) septa and costae can be less than half as thick as major septa. This character was used by Duncan (1863, 1864) to distinguish various forms of *Hadrophyllia*, *Thysanus* and *Manicina*. *States*: 0 = equal; 1 = unequal.

10. *Coenosteum.* Coenosteum is skeleton deposited by coenosarc tissues. In meandroid forms, coenosteum develops between adjacent series and reflects the complex packing of the meander network. In colonies restricted to only uni-directional or bi-directional budding (character 4), adjacent corallites are always sister polyps, so the development of coenosteum is geometrically forbidden. Therefore, taxa with restricted budding geometry are scored as 'absent'. Similarly, by definition, coenosteum is undeveloped in phaceloid colonies, and these taxa have been scored as 'absent'. No attempt was made to distinguish between these two character states to avoid overweighting the distinction between colony forms included as other characters. Transitions among the character states are not restricted to a linear sequence (e.g. it is possible to proceed from an absent coenosteum to a wide coenosteum without intermediate steps), so this character was left unordered. Coenosteum is invariably present or absent, but its width can be related to the stage of formation of a new bud. Therefore, maximum coenosteum widths were used when coding the character. *States*: 0 = absent; 1 = present with adjacent walls; 2 = present and narrow (less than meandroid valley width); 3 = present with medium width (equal to meandroid valley width); 4 = present and wide (greater than valley width).

11. *Exothecal dissepiments.* This character indicates the presence and relative abundance of tabular or vesicular horizontal structures extending between costal plates. Several taxa have been scored as 'missing' because of a shortage of well-preserved material in the current collection. *States*: 0 = absent; 1 = present.

12. *Continuity of costae.* A score for this character was determined by whether or not costae (or septa) are continuous between adjacent meander series. It is meaningless for flabellate or phaceloid colony forms and has been coded as 'missing' for several taxa. In meandroid forms, this character can in part reflect the relative sinuosity and proximity of the meander series to neighbouring series,

and possession of confluent septa suggests greater colony integration among adjacent meander series (Coates and Oliver 1973). *States*: 0 = discontinuous; 1 = continuous.

13. *Number of septal cycles*. The number of septal cycles has long been recognized as a significant character in corals. In forms with corallites formed by extramural budding, it can more easily scored by counting septa, but in meandroid forms the relative lengths and widths of septa must be examined. This character is related to septal spacing (character 14). *States*: 0 = three complete; 1 = more than three complete; 2 = nearly four complete; 3 = four or more complete.

14. *Septal spacing*. This character is scored using the number of septa per 5 mm along a meander series. It is related to septal width and the number of septal cycles. Because it is a relatively continuous character, discrete levels were assigned through visual inspection on a range of septal spacing measured on type material or taken from species descriptions (Text-fig. 1). Divisions were made between six and 12 septa per 5 mm reflecting discontinuities in the distribution at those points. Some taxa had overlap between adjacent character states. *Manicina puntagordensis*, *Favia leptophylla* and *F. macdonaldi* were scored as having fewer than six septal per 5 mm and *Colpophyllia elegans* was scored as having more than 12 septa per 5 mm. An alternative analysis with these four taxa scored between six and 12 septa per 5 mm did not change the hypothesized relationships among the taxa. *States:* septa per 5 mm: 0 = less than six; 1 = between six and 12; 2 = more than 12.

15. *Equality of septal thickness*. Major septa are generally longer than minor septa, and they may be thicker. In taxa with septothecal wall structures, this character should be structurally related to costal thickness (character 9), but often costae are equal and septa are unequal. *States*: 0 = equal; 1 = unequal.

16. *Columella width*. This character describes the width of the columella relative to the overall valley width. Absolute columella width is likely to be structurally correlated with overall valley width (character 7), so relative width was scored to avoid implicitly over-weighting corallite size. *States*: 0 = less than or equal to one-quarter valley width; 1 = one-third valley width; 2 = one-half width or wider.

17. *Columella continuity*. In meandroid colonies, the columella can be an continuous structure, with no easily recognizable corallite centres. But, in some taxa, corallite centres are clearly evident from the degree of septal inflection and by breaks in the columella. These breaks are often more clearly demonstrated in taxa with reduced or poorly developed columella and may be related to the process of budding. *States*: 0 = continuous; 1 = discontinuous.

18. *Septal lobes*. There is a great deal of confusion regarding septal and paliform lobes (character 19). As used here, septal lobes can only be found on lamellar septa composed primarily of a single fan system of simple trabeculae. Septal lobes are internal lobes formed by a second fan system. In contrast, paliform lobes are vertical extensions of septa formed by one or more trabecular bundles, and not generally composed of a second fan system. Some workers (Chevalier 1975; Veron *et al.* 1977) considered the presence of well-developed septal lobes to be significant, and based the definition of a new scleractinian family (Trachyphyllidae) largely on this character. However, this characteristic is widespread within the taxa considered here even though they are classified as members of the Faviidae. *States*: 0 = absent; 1 = present.

19. *Paliform lobes*. Paliform lobes are vertical extensions of the medial margins of septa formed by one or more trabeculae. They are not true pali because they do not form through the process of septal substitution (Wells 1956), in which the medial margin of a exoseptum bifurcates as it grows upwards and new septa are inserted into the calice. Paliform lobes are distinguished from septal

lobes by forming from a single or multiple trabeculae which are not arranged as a fan system. In general, paliform lobes are vertical extensions of skeleton with margins that are free from the parent septum, and are usually associated with a thickening of the inner ends of septa. Although these structures are considered distinct from septal lobes (character 18), they may represent proto-septal lobes. However, they have been coded as distinct because no specimens examined in this study have both well-developed septal and paliform lobes. *States*: 0 = absent; 1 = present.

20. *Endothecal dissepiments*. These structures are similar to exothecal dissepiments, but develop internally. *States*: 0 = absent or very few; 1 = intermediate; 2 = abundant.

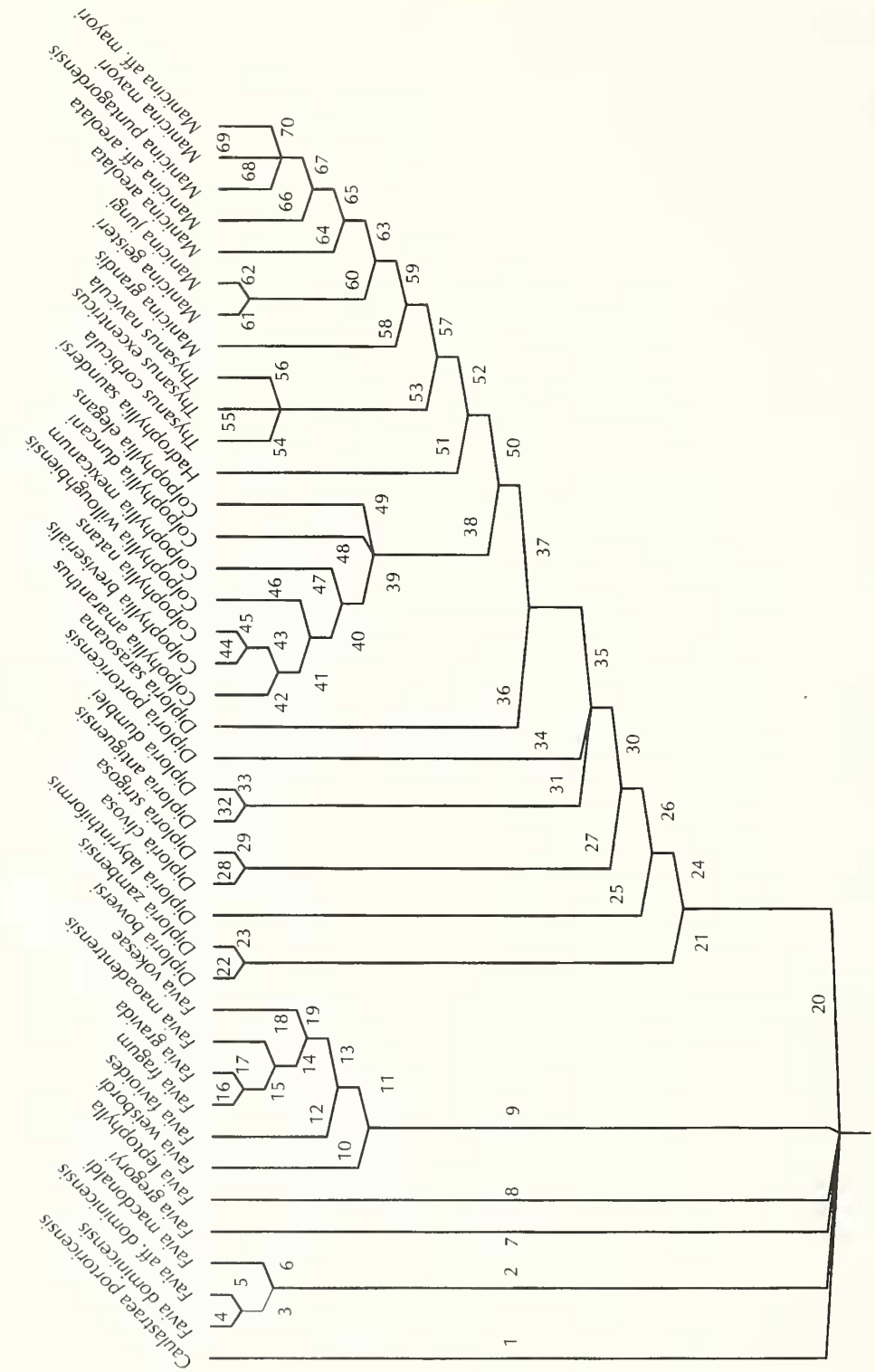
21. *Wall structure*. Two distinct wall structures have been recognized in the study taxa. In all cases, septo-costal plates extend across the theca, but the margins of calices are defined by different structures. Septotheca is formed by septal skeleton and develops as a thickening and fusing of adjacent septo-costal plates. In contrast, thecal skeleton may not be not genetically related to the septa, in which case the theca is constructed by abundant and closely spaced dissepiments. This style of wall is termed paratheca (Wells 1956). *States*: 0 = septothecal; 1 = parathecal.

22. *Double or single wall*. In some parathecate colonies, wall development between adjacent meander series appears to be co-ordinated resulting in a distinctive double wall structure. In these forms, the walls appear as clearly defined thin plates separated by a constant distance. Although this character applies only to parathecal forms, it was scored for all taxa. This will increase the relative weight of wall structures in the phylogenetic inference. *States*: 0 = single wall; 1 = double wall.

23. *Size of colony*. Although colony growth is indeterminate, some species of corals tend to have smaller maximum colony sizes than others. This is no doubt a reflection of the life history or environmental tolerences of taxa, with some forms that utilize clonal reproduction through fragmentation possessing large (although not necessarily connected) colonies. Other taxa are rarely found as large colonies, especially free living species which depend on some degree of mobility to survive in sediment-rich environments (Johnson 1992). Although maximum colony size is clearly a continuous character, no effort was made here to define size categories statistically. Categories were defined by roughly dividing the total range of size variation of all known Neogene Caribbean coral taxa into three groups (Budd *et al.* 1994). *States*: 0 = small ($< 0{\cdot}1$ m); 1 = intermediate (0·1–0·3 m); 2 = large ($> 0{\cdot}3$ m).

Phylogenetic inference

Paup version 3.1.1 (Swofford 1993) was used to find the most parsimonious trees which describe the relationships among the taxa. Because of the relatively large number of taxa, a heuristic search was performed followed by total branch swapping of the set of all shortest unrooted trees. The maximum number of trees held in memory was 2000. The initial trees were found using random addition sequence with 100 iterations to help assure that the identified trees were close to global minima. Once the set of minimum trees was found, the tree was rooted and character state reconstructions were calculated relative to an outgroup consisting of *Caulastraea portoricensis*. Both Matthai (1928) and Wells (1956) present hypotheses of 'morphogenetic trends' in colonial corals with colonies formed by primarily extratentacular budding plesiomorphic to meandroid and flabellate colonies formed by exclusively intratentacular division. *Caulastraea* is the only genus in the Faviidae characterized by phaceloid colonies (Veron *et al.* 1977) and therefore most probably is part of a more pleisiomorphic lineage of the family than the other lineages included in this study. Extant species of *Caulastraea* are widely distributed across the Indo-Pacific region (Veron 1993) and have occurred since the Oligocene in the Caribbean, Indo-Pacific and Mediterranean regions (Chevalier 1961; Frost and Weiss 1979; Pfister 1980; Budd *et al.* 1994). Therefore, as a group,



TEXT-FIG. 3. Strict consensus tree calculated from 78 trees with length 175. The relationships among species are ambiguous at three nodes. Apomorphies and support indices associated with branches are included as Table 2.

Caulastraea species are among the most widespread of all faviid corals. Strict consensus trees were formed from multiple equally parsimonious trees, and characters were optimized on the consensus cladogram assuming accelerated character transformation.

A cladistic permutation tail probability test (PTP) was used to assess the phylogenetic signal in the character matrix (Archie 1989; Faith and Cranston 1991). This test is a comparison of the length of the observed shortest tree with tree lengths for a set of 100 character matrices obtained by randomly reassigning character states for each taxon. The PTP test is designed to examine the amount of cladistic covariation in the data. The analysis was performed using code written by me for the automatic scripting of PAUP commands in NEXUS format. For each randomized data set, a heuristic search was used so the estimate of minimum tree length for each iteration is conservative.

The PTP test suggests that significant phylogenetic signal exists in the character matrix, with the observed most parsimonious tree shorter than 99 replicate trees ($P = 0{\cdot}01$). The initial heuristic search identified 78 equally parsimonious trees each with 175 steps. Five ambiguous nodes exist on a strict consensus of these trees (Text-fig 3); the relationships among some *Favia* species and the outgroup are not well resolved. Similarly, the relationships among *Colpophyllia elegans*, *C. duncani* and a group containing the other *Colpophyllia* species are not resolved. The relationships among *Manicina mayori*, *M. puntagordensis*, and *M.* species B and the relationships among the three *Thysanus* species are also not resolved. Some polytomies might be expected if several new lineages originate from another lineage which is not evolving new apomorphies, so further manipulation of the characters (e.g. reweighting) to increase resolution was not attempted.

Two randomization tests were also applied to assess the support for hypotheses of group monophyly. The 'evolutionary bootstrap' works by finding maximally parsimonious trees for a series of pseudo-random replicates of a character matrix constructed by randomly resampling (with replacement) the vector of character states for each taxon (Felsenstein 1985). The proportion of these trees which include a particular monophyletic group is used as a measure of support for that group. There may be serious objections to this test (reviewed by Sanderson 1995), but it is widely used in molecular systematics where large numbers of characters are available. Bootstrap support estimates were obtained using the Random Cladistics program with 100 pseudoreplicates (Siddall 1995).

Clade stability was also assessed using a modified jackknife procedure in which a series of cladograms were constructed for subsets of taxa with each taxon removed (Lanyon 1985). This is a way of examining the effects of individual taxa in the analysis. Although a different version of this test can be performed using the Random Cladistics package, this analysis was performed using a scripting program written by the author. Jackknife support values were calculated by determining group frequency from a total of 39 replicate trees constructed using heuristic searches. In each replicate, *Caulastraea portoricensis* was left in the analysis as the outgroup. If multiple shortest trees were found, a strict consensus tree was calculated for that replicate. The frequency distribution of all possible groups of taxa defined in the all-taxon consensus tree was then derived from the 39 replicate consensus trees by counting the number of trees in which each group was defined. The total number of iterations in which a group could possibly be found is equal to the number of iterations minus the number of taxa in the group, because if a taxon is not included in the analysis, it will not occur in the resulting tree. Jackknife percentages for each group were calculated by dividing the frequency of each group by the number of trees in which the group could possibly have occurred, the higher the percentage, the more stable the group to the effects of missing or 'problematical' taxa.

Character state reconstruction on the consensus tree is ambiguous for nine characters (Table 1). The tree as a whole has low consistency (rescaled consistency index = 0·14; retention index = 0·78), but high homoplasy levels are in part related to the large number of taxa included in the analyses (Sanderson and Donoghue 1989). Homoplasious characters include septal and costal architecture, but characters associated with budding and the corallite wall and columellae provide more support for the consensus tree. Contrary to expectation, results of a Kruskal–Wallace rank sum test suggest that discrete characters are not more consistent with the consensus cladogram than continuous characters ($\chi^2 = 0{\cdot}53$; 1 d.f. $P = 0{\cdot}47$).

TABLE 2. Branch stability measures and apomorphies for branches. Branch numbers refer to Text-figure 4. Jackknife frequencies and are shown with the maximum number of replicates for each group indicated in parentheses. Character states were optimized on the cladogram assuming accelerated change, and ambiguous apomorphies indicated by asterisk.

Branch	Jackknife	Apomorphies
1	—	6 (1–0), 8 (1–0), 10 (3–0), 11 (1–0), 13 (1–2), 16 (1–0), 19 (1–0), 23 (1–2)
2	0·69 (36)	10 (3–1)*, 12 (0–1), 16 (1–2)*, 20 (0–2)
3	0·76 (37)	19 (1–0), 21 (0–1)
4	—	6 (1–0), 10 (1–2)*
5	—	23 (1–0)
6	—	7 (1–2), 10 (1–4)*, 14 (1–0)
7	—	8 (1–0), 13 (1–0), 14 (1–0), 19 (1–0), 20 (0–2)
8	—	6 (1–0), 7 (1–0), 8 (1–2), 14 (1–0), 22 (0–1)
9	0·89 (33)	14 (1–2), 15 (1–0)*, 16 (1–2)*
10	—	13 (1–0)
11	0·97 (34)	7 (1–0), 10 (3–2), 23 (1–0)
12	—	4 (2–1)
13	0·97 (35)	13 (1–3), 15 (0–1)*, 19 (1–0)
14	0·53 (36)	6 (1–0), 9 (0–1)
15	0·51 (37)	8 (1–2)
16	—	13 (3–2), 14 (2–1)
17	—	3 (0–1), 16 (2–1)
18	—	1 (1–0), 10 (2–4), 20 (0–1)
19	—	10 (2–1), 12 (0–1)
20	0·64 (11)	3 (0–1), 10 (3–4), 15 (1–0), 16 (1–2)*, 20 (0–1)*
21	0·59 (37)	13 (1–0)
22	—	7 (1–0), 12 (0–1), 14 (1–0), 16 (2–1)*
23	—	19 (1–0)
24	0·53 (13)	3 (1–2)
25	—	—
26	0·50 (14)	5 (1–0), 10 (4–1)
27	0·97 (37)	11 (1–0), 15 (0–1), 23 (1–2)
28	—	7 (1–0), 8 (1–0), 13 (1–2), 14 (1–2)
29	—	12 (0–1)
30	0·44 (16)	16 (2–1)*, 20 (1–2)*
31	0·97 (37)	6 (1–0), 7 (1–0), 23 (1–0)
32	—	8 (1–2), 2 (1–3), 14 (1–2), 15 (0–1)
33	—	10 (1–3), 12 (0–1)
34	—	—
35	0·53 (19)	6 (1–2), 8 (1–0), 12 (0–1)
36	—	13 (1–0), 20 (2–0)
37	0·80 (20)	7 (1–2), 16 (1–0), 19 (1–0), 21 (0–1)
38	0·97 (32)	2 (1–2), 13 (1–2), 15 (0–1), 17 (0–1)
39	0·82 (34)	5 (0–1)*, 10 (1–2), 22 (0–1)
40	0·83 (35)	3 (2–1), 7 (2–3)
41	1·00 (36)	5 (1–0)*, 12 (1–0), 13 (2–1), 14 (1–0), 15 (1–0), 19 (0–1)
42	—	6 (2–3)
43	0·84 (37)	23 (1–2)
44	—	—
45	—	3 (1–2)
46	—	13 (2–3), 14 (1–2)
47	—	—
48	—	—
49	—	7 (2–1), 14 (1–2)

TABLE 2. (*cont.*)

Branch	Jackknife	Apomorphies
50	0·96 (27)	1 (1–0), 3 (2–3), 4 (2–1), 10 (1–0), 23 (1–0)
51	—	7 (2–3), 14 (1–0)
52	0·50 (28)	5 (0–1), 6 (2–1)
53	0·58 (36)	2 (1–0)*, 4 (1–0)*, 6 (1–0)*, 11 (1–0), 19 (0–1), 20 (2–0)
54	—	9 (0–1), 13 (1–3), 14 (1–2), 15 (0–1)
55	—	2 (0–1)*, 5 (1–0), 6 (0–1)*
56	—	4 (0–1)*, 20 (0–1)*
57	0·48 (31)	8 (0–2), 18 (0–1)
58	—	—
59	0·44 (32)	9 (0–1)*, 15 (0–1)
60	0·54 (37)	13 (1–2)
61	—	2 (1–2), 5 (1–0), 6 (1–2), 7 (2–3), 8 (2–1)
62	—	13 (2–3), 14 (1–2), 18 (1–0), 19 (0–1)
63	0·85 (34)	2 (1–0), 4 (1–2), 10 (0–2), 16 (0–1)
64	—	12 (1–0), 20 (2–1)
65	0·54 (35)	6 (1–3), 9 (1–0)*
66	—	—
67	0·92 (36)	1 (0–1)*, 5 (1–0)*, 7 (2–3), 22 (0–1), 23 (0–1)
68	—	1 (1–0)*, 6 (3–2), 14 (1–0)
69	—	5 (0–1)*, 9 (0–1)
70	—	15 (1–0), 16 (1–0)

Groups

The consensus tree suggests a distinct *Favia* subgroup, including *Favia maodentrensis*, *F. favioides*, *F. fragum*, *F. gravida*, and *F. vokesae*. This group is supported by three unambiguous apomorphies and can be found in a high proportion of the jackknife trees (Table 2). The shortest tree which does not include this group is two steps longer than the current hypothesis, and the three characters which support this group all have greater than median rescaled consistency indices. The group is characterized by decrease in both corallite and colony size and a narrowing of the coenosteum.

A second group, including *Colpophyllia*, *Hadrophyllia*, *Thysanus* and *Manicina* species, is also well supported. Apomorphies include deeper calices, a reduced epitheca, and the development of confluent costae. However, jackknife support for this group is not as strong as for some of the other groups, and only one additional step is required for an hypothesis which does not include this clade. Within this large group, two main subgroups are defined, one including the *Colpophyllia* species and the other including *Hadrophyllia*, *Thysanus* and *Manicina* species. Jackknife frequency for the *Colpophyllia* clade is very high (0·97) and the shortest tree which does not include the group is two steps longer than the current hypothesis. The *Colpophyllia* clade is supported by four unambiguous character state changes including the development of sinuous meandroid series, the insertion of minor septa which are thinner than the major septa. Most importantly, the *Colpophyllia* clade is characterized by the development of a discontinuous columella.

A smaller subgroup is stable within the *Colpophyllia* clade. This group includes the three Neogene species *Colpophyllia natans*, *C. amaranthus* and *C. breviserialis*, and is defined by a total of six character state changes, one of which is ambiguous. This is the most stable group in the current hypothesis, with support from all possible jackknife trees. This group is supported by a loss of fourth order septa, which results in a decrease in septal number accompanied by an increase in septal spacing, as well as the loss of septa with unequal thickness. Paliform lobes can be identified in all three Neogene *Colpophyllia* species. All of these characters are highly homoplasious with

rescaled consistency indices less than 0·10, demonstrating that homoplasious characters can be used to substantiate stable groups.

A group including species of *Manicina*, *Hadrophyllia* and *Thysanus* (MHT) is supported by five apomorphies, including the development of a free-living mode of growth and generally smaller colonies and the cessation of wall development between newly budded polyps. New buds are constrained to a linear series with no branching or forking resulting in a flabellate growth form and loss of coenosteum. These characters are related to loss of attachment to the substrate. Previous work has shown that colony size in the extant free-living coral *Manicina areolata* is constrained by the ratio of tissue surface area to colony mass (Johnson 1992) so that large colonies experience high mortality rates due to reduced colony mobility. Adopting a free-living mode allowed these taxa to occupy sediment-rich reef marginal environments equivalent to shallow or deep seagrass beds and mangrove fringe systems.

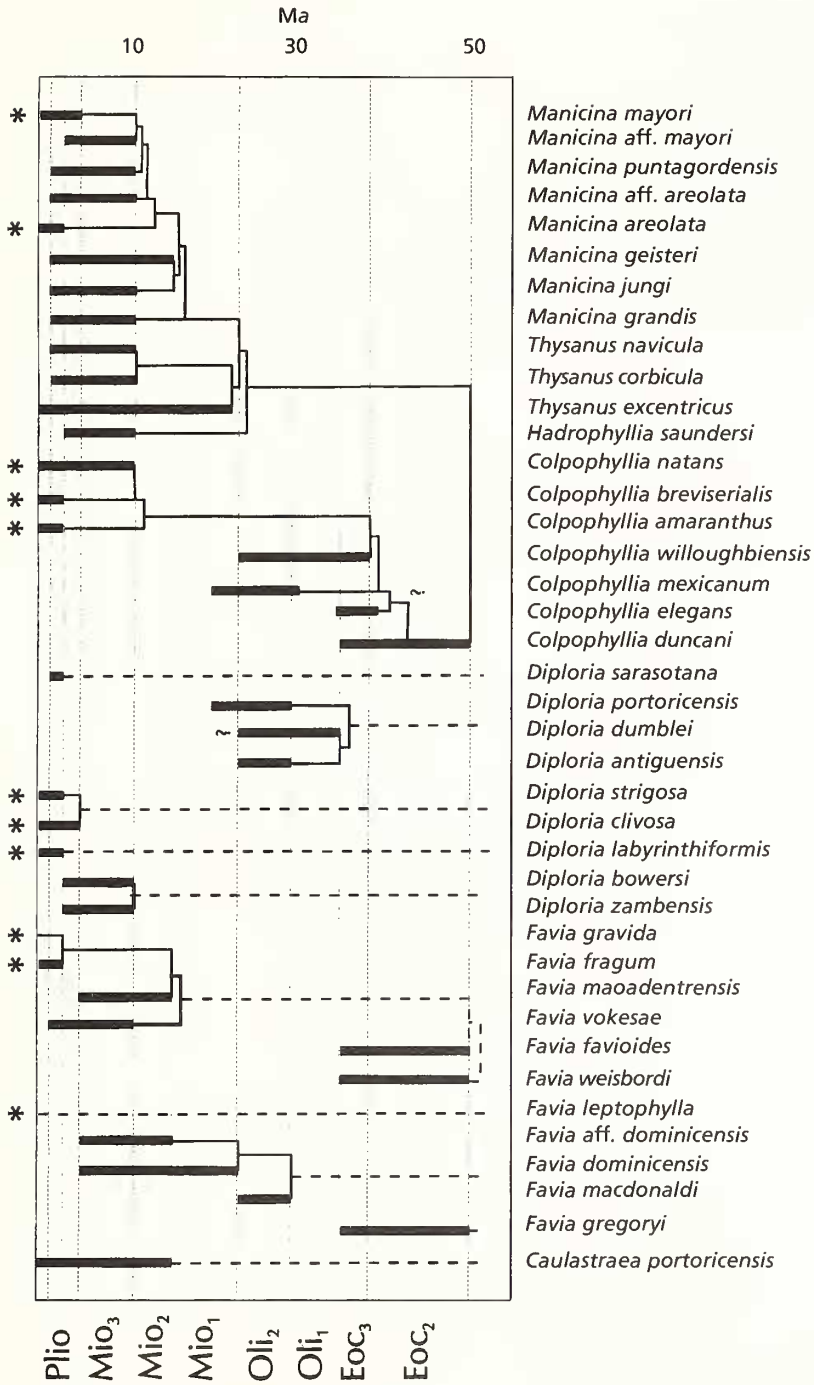
Stable subgroupings can be recognized within the MHT group. One node defines a group including the five meandroid *Manicina* species. This node is supported by four unambiguous apomorphies, and is characterized by the reacquisition of branched meandroid series with straight meander valleys between branch points accompanied by coenosteum development between adjacent branches. These characters are all more consistent with the hypothesis than average. However this group has relatively low jackknife support (0·85) and only one step is required for a tree which does not include the group. A second subgroup has high jackknife support (0·92) and includes three meandroid *Manicina* species with attached colonies. These taxa are also characterized by intermediate colony size and deeper calices with steeply sloping septal margins.

EVOLUTIONARY TREE

An evolutionary tree was constructed by superimposing cladistic relationships on to the stratigraphical range of species whilst minimizing hypothetical range extensions (Text-fig. 4). A single tree was selected from the set of most parsimonious trees by resolving ambiguous nodes using stratigraphical information (Smith 1994). The three ambiguous nodes in the more apomorphic part of the tree were treated first. For the ambiguous node in the *Colpophyllia* group, *C. duncani* was selected as the sister taxon to a group including *C. elegans* and the other *Colpophyllia* species. The alternative hypothesis places *C. elegans* as the pleisomorphic sister group to *C. duncani* and the other *Colpophyllia* species, and requires a range extension for *C. elegans* through the Mid Eocene. Similar reasoning was used to resolve the *Thysanus* and *Manicina* ambiguous nodes. A group including *Thysanus corbicula* and *Thysanus excentricus* is the hypothetical sister group of *Thysanus navicula*, and *Manicina puntagordensis* is identified as the pleisomorphic sister taxon to a group including *M. mayori* and *M.* aff. *mayori*. An ambiguous node involving the three Oligocene *Diploria* species was resolved by inferring a hypothetical monophyletic group including all three taxa. The alternative relationship identified two distinct stem groups, one including *D. antiguensis* and *D. dumblei* and the other including only *D. portoricensis*. The addition of stratigraphical information was not able to resolve the remaining ambiguous node which appears along the *Favia* stem groups. A single tree was selected from two remaining hypotheses which suggests that a group including *Favia dominicensis*, *F.* aff. *dominicensis*, and *F. macdonaldi* is a sister group to *F. gregoryi*.

The tree includes several hypotheses of ancestry when no apomorphies occur along cladogram branches. For example, *Colpophyllia breviserialis* is identified as the ancestor of *C. natans* because no autapomorphies are hypothesized for *C. breviserialis*. Branching events are drawn at or below boundaries for convenience; they are assumed to have occurred sometime within the time interval after the boundary. Last occurrences of taxa which are drawn at boundaries also reflect imprecise age assignment, and actual extinctions are assumed to have occurred in the time interval prior to the boundary.

Major range extensions are required for the more pleisomorphic taxa, and multiple origins of *Favia* and *Diploria* lineages are suggested. *Favia* is widely dispersed in both time and space. The genus has been described from the Cretaceous of Europe and the Caribbean (Vaughan and Wells



TEXT-FIG. 4. Evolutionary tree created by superimposing the selected cladogram onto stratigraphical ranges of the study taxa whilst minimizing hypothesized range extensions. Asterisks indicate extant species.

1943), and has developed a pan-tropical distribution since that time (Pfister 1980; Budd *et al.* 1992; Budd *et al.* 1994). The biogeographical origins of the distinctive coral fauna of north-eastern Brazil has never been demonstrated conclusively (Laborel 1967). However, this phylogeny suggests that the two endemic *Favia* species, *F. leptophylla* and *F. gravida*, are not closely related. Their most common ancestor is likely to be an unknown Paleogene species. Therefore, the biogeographical origins of this fauna is complex, including repeated migration of coral species from into and out of Caribbean and Brazilian reef communities.

As currently recognized, *Diploria* is also a paraphyletic group. Frost (1977) suggested close similarities among several Mediterranean and Caribbean species of *Diploria*, and species described from the Oligocene of Europe (Vaughan and Wells 1943; Pfister 1980) have been placed in the genus. However, the European forms have discontinuous columellar structures, and may represent a different lineage than the Caribbean forms (Chevalier 1961; Budd and Johnson 1998). Neogene *Diploria* species are restricted to the Caribbean region, but it is unlikely that the Miocene and later Caribbean *Diploria* species were directly derived from the Oligocene species.

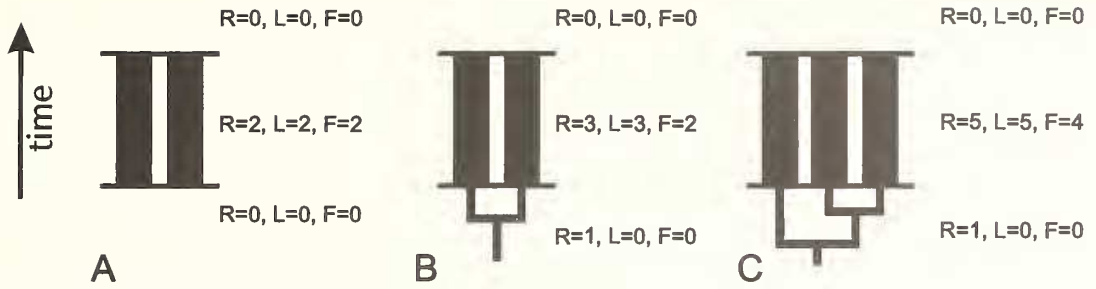
In contrast, there is strong evidence of monophyly for both *Colpophyllia* and the MHT group. *Colpophyllia* was abundant in Europe during the Oligocene (Pfister 1980) and Miocene (Chevalier 1961), but became restricted to the Caribbean in the Neogene. The tree suggests that the Neogene Caribbean lineage originated from within the Paleogene lineage and has remained isolated from the Mediterranean fauna. No species of *Manicina*, *Hadrophyllia* or *Thysanus* has been described from outside the Caribbean, so a hypothesis of monophyly for this group is supported by the distribution data.

LATE NEOGENE TURNOVER

The evolutionary tree was used to compare evolutionary rates both with and without phylogenetic information. Phylogeny has two main effects on the distribution of taxa through time. First, the timing of species origination may be extended below the first occurrence of the species in the record, resulting in an hypothetical range extension. These range extensions will only alter estimates of origination rates and total species richness in earlier time intervals; they can have no effect on estimates of extinction rates. A phylogeny can also suggest the presence of undiscovered ancestral taxa termed 'ghost lineages' (Norell 1992). These are lineages predicted by tree topology. Since the age of both first and last occurrence of ghost lineages can be estimated on the evolutionary tree, including ghost lineages can alter estimates of species richness, origination and extinction through time.

Taxonomic turnover was analysed using standard techniques (Gilinsky 1991). The study interval has been divided into nine time periods of roughly equal duration, and an estimate of total species richness was obtained by counting the number of lineages which occur within or both before and after each interval. Some conventions were adopted to estimate the number of first and last occurrences in each time interval, so that first occurrences which correspond to boundaries are attributed to the interval after the boundary, but last occurrences mapped on to a boundary are attributed to the interval prior to the boundary (Text-fig. 5). All ghost lineages are counted if they were supported by at least one apomorphy. If both sister lineages associated with a branching event are supported by an apomorphy, then the branching event is assumed to be associated with the extinction of the parent lineage. If one of the sister lineages is not supported by an apomorphy, then it is assumed to be the parent lineage. Therefore, most branching events result in two first occurrences and one last occurrence. Proportional rates are used to estimate the magnitude and timing of taxonomic turnover. These are calculated as the number of first and last occurrences divided by the taxonomic richness within each time interval. Under a wide range of extinction models, these estimates of true branching and extinction rates are likely to be biased by differences in interval duration, but no individual metric has been proposed that provides unbiased estimates under a range of typical extinction models (Foote 1994).

As expected, the addition of ghost lineages increased estimated richness (Text-fig. 6A), with the

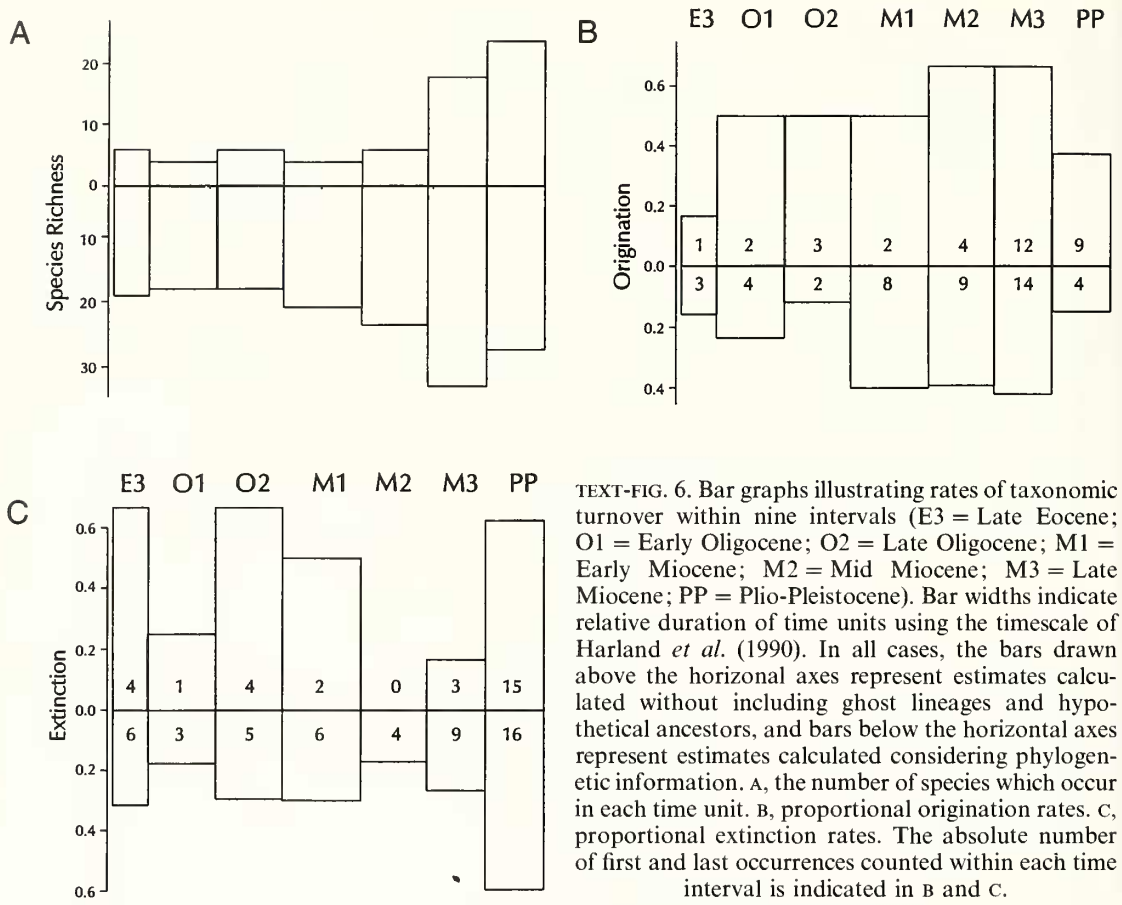


TEXT-FIG. 5. Rules for counting species richness and the number of first and last occurrences with and without hypothetical ancestors. In each case, vertical bars represent species ranges and horizontal lines are boundaries of stratigraphical intervals. Parts B and C include hypotheses of relationships and ghost lineages. A, when first occurrences are associated with interval boundaries, the species is assumed to have originated after the boundary, but last occurrences at boundaries are attributed to the prior time interval. B, hypothetical ancestors are assumed to become extinction during cladistic branching. C, all hypothetical ancestors are considered when multiple taxa appear to arise simultaneously.

long branches in the *Favia* and *Diploria* taxa increasing apparent richness during the Paleogene and Early Miocene. The general pattern remains unchanged with richness reaching a peak in the Late Miocene and Plio-Pleistocene faunas, but the highest total richness estimated including ghost lineages occurred during the Late Miocene with a decrease in richness during the Pliocene and Pleistocene. The number of first appearances (Text-fig. 6B) is also increased when phylogenetic predictions are included, but the overall pattern of high numbers of first appearances in the late Miocene is similar with and without ghost lineages. This increase might be caused by the increase in species richness during the Late Miocene. Proportional origination rates estimated including phylogeny suggest high origination throughout the Miocene. Patterns of species extinction through time are not changed by including phylogenetic information in the analysis. The estimates of pre-Pliocene background extinction rates are lower due to increased richness estimates when ghost lineages are counted, but neither the timing nor the magnitude of the Plio-Pleistocene extinction event is significantly altered. Including the ghost lineages has increased the relative difference between the Plio-Pleistocene time of species extinction relative to background extinction. For this group of reef-corals, there was radiation throughout the Miocene resulting in an increased number of species until the late Miocene. However, during the Plio-Pleistocene, most of the taxa suffered extinction.

Although the addition of phylogeny did not cause substantial change to the results of the analysis of taxonomic turnover, it does allow identification of periods with poor sampling, especially for the *Favia* and *Diploria* species during the Oligocene and early Miocene. Examination of the evolutionary tree also facilitates identification of potentially problematical occurrences of particular taxa. For example, the first appearance of *Thysanus excentricus* in the lower Miocene results in considerable range extension for the MHT lineage. As the database is refined, this occurrence will be examined in detail to insure that both the age assignment and identification are correct.

Therefore, although adding phylogenetic information to stratigraphical ranges can aid the detection of periods of poor sampling, the approach suffers from several potential sources of error. Most serious is the requirement for a stable phylogenetic hypotheses. This may not be possible for some problems, especially for large datasets or for groups without clearly defined discrete morphological characters. Alternate methods for detecting uneven sampling exist for such cases. For example, a sample completeness index can be calculated as the ratio of the number of taxa found in a particular interval to the number which occur both before and after the interval. A



TEXT-FIG. 6. Bar graphs illustrating rates of taxonomic turnover within nine intervals (E3 = Late Eocene; O1 = Early Oligocene; O2 = Late Oligocene; M1 = Early Miocene; M2 = Mid Miocene; M3 = Late Miocene; PP = Plio-Pleistocene). Bar widths indicate relative duration of time units using the timescale of Harland *et al.* (1990). In all cases, the bars drawn above the horizonal axes represent estimates calculated without including ghost lineages and hypothetical ancestors, and bars below the horizontal axes represent estimates calculated considering phylogenetic information. A, the number of species which occur in each time unit. B, proportional origination rates. C, proportional extinction rates. The absolute number of first and last occurrences counted within each time interval is indicated in B and C.

combination of phylogenetic information and such phylogeny-free completeness indices will lead to a better understanding of the potential for uneven sampling to result in spurious patterns of taxonomic turnover.

SUMMARY

1. A new phylogeny for Caribbean faviid corals constructed from both continuous and discontinuous skeletal characters results in the definition of several lineages. One group includes all *Colpophyllia* species and another includes *Manicina*, *Hadrophyllia* and *Thysanus*. Within these groups the Neogene *Colpophyllia* species and the *Manicina* species with attached colonies are stable subgroups.

2. As currently recognized, *Diploria* and *Favia* are paraphyletic with respect to the meandroid taxa. This may be related to their biogeography with repeated migrations in and out of the Caribbean basin.

3. An evolutionary tree requires much hypothetical range extension for the poorly resolved taxa, but there is substantial agreement between branching order and order of first appearance within the *Colpophyllia* and *Manicina* groups.

4. Analysis of the rates of taxonomic turnover including ghost lineages and range extensions do not change the pattern detected when phylogenetic information was not included in the analysis; however, the evolutionary tree is useful in highlighting periods of relatively poor sampling and problematical occurrences of particularly sensitive taxa.

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